Subterranean Biology 49: 19–29 (2024)
doi: 10.3897/subtbiol.49.121747
https://subtbiol.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Subterranean Biology
Published by The International Society for Subterranean Biology

Cavefish dorsoventral axis angle during wall swimming: laterality asymmetry

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Academic editor: Maria Elina Bichuette | Received 26 February 2024 | Accepted 3 May 2024 | Published 23 May 2024

https://zoobank.org/8651000A-CB5F-4D73-9967-1D82A5BBF0B3

Citation: Espinasa J, Espinasa L (2024) Cavefish dorsoventral axis angle during wall swimming: laterality asymmetry. Subterranean Biology 49: 19–29. https://doi.org/10.3897/subtbiol.49.121747

Abstract

The *Astyanax* fish exhibits two morphs: an eyed, pigmented surface morph and an eyeless, depigmented cave morph. Previous studies have shown that blind morphs swim nearly parallel to the wall and can sense detailed information about objects by gliding alongside them and sensing changes in the flow field around their body using their lateral line sensory system. Hence, cavefish can build hydrodynamic images of their surroundings. Field observations showed that one of their presumptive prey, mysid shrimp, is predominately found not on the floor, but crawling on the walls. In our study, the angle of the body axis with respect to a vertical wall was measured while fish swam in a tank. Results show that when swimming by a wall, cavefish incline the vertical axis of their body away from the wall. But most significantly, this angle is different when the right side or the left side of their body is oriented towards the wall. Intriguingly, cavefish have a leftward-biased dorso-cranial bend, where the convex side of the head is towards their right side. Other studies have shown behavioral "handedness". When exhibiting Vibration Attraction Behavior (VAB), cavefish in the field show laterality on the preponderant side they circle to explore a vibrating stimulus. Likewise in larval prey capture (LPC) behavior, larvae strike towards prey preferentially located on one side. Our results support that cavefish also express behavioral lateralization during passive swimming by walls and/or when searching for food that is perched on the walls, such as mysid shrimp.

Keywords

Biomechanics, El Abra, handedness, stygobites, troglomorphy

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Introduction

The *Astyanax* fish belongs to the Characidae family. It has an eyed morph that lives in surface streams and an eyeless morph that has evolved in subterranean environments, where light is absent, and food resources are often distributed unevenly (Espinasa et al. 2017). The *Astyanax* cavefish has garnered significant attention in the scientific community due to its unique ecological niche and remarkable adaptations. The way it navigates its surroundings in the absence of vision and the feeding posture with which it searches for food while swimming stand out as crucial components of its adaptive strategy (Schemmel 1980). Understanding these dynamics sheds light on the evolutionary processes that have shaped this species and offers valuable insights into the broader field of adaptive behavior in aquatic organisms.

Studies suggest that the *Astyanax* cavefish employs a range of feeding behaviors, which are modified depending on the nature of available food and the environmental local conditions (Espinasa et al. 2021). This adaptive flexibility suggests a sophisticated sensory-motor integration that allows them to efficiently navigate and locate food sources in their subterranean habitat. For example, an increase in the number of their head neuromasts is responsible for the emergence of VAB (Yoshizawa et al. 2010) and an increase in the number of serotonin neurons in the cavefish hypothalamus is responsible for their persistent food-searching behavior (Elipot et al. 2014). Unraveling the basis of these behaviors not only enhances our understanding of the species but also provides valuable comparative insights into the evolution of feeding strategies across different aquatic environments.

To cope with the challenges of foraging in such environments, these fish have developed specialized feeding behaviors that optimize their chances of locating and capturing prey. The posture and the angle at which *Astyanax* cavefish search for and pick up food lying in the bottom of the tank have been identified as a critical aspect of their feeding behavior. As seen in Fig. 1A–C, surface fish fed at a high average angle from the horizontal (average 74°), while two populations of cavefish, the Pachón cavefish (38°) and the Tinaja cavefish (49°), fed at significantly lower angles (Kowalko et al. 2013). This behavioral change in feeding posture is not due to changes in cranial facial morphology, body depth, or to take advantage of the expansion in the number of taste buds (Kowalko et al. 2013). Quantitative genetic analysis showed that two different cave populations have evolved similar feeding postures through a small number of genetic changes, some of which appear to be distinct (Kowalko et al. 2013).

Foraging behavior has also been described when food is floating on the surface. Cavefish respond to the vibrations generated by a potential prey by approaching using the neuromasts of the left side of their face or their right side followed by highly responsive circling (Espinasa et al. 2022). Of notice, different cave populations showed in the field different "handedness", expressed by preferentially circling to the right side or the left side. Likewise, in LPC behavior, cavefish larvae from different populations strike at prey that is preferentially on their right side or their left side.

While foraging behavior has been described for food on the bottom of the floor and the surface, such behavior has not been described for food on the walls. That blind cavefish exhibit a preference for remaining near the walls of a novel enclosure was noted

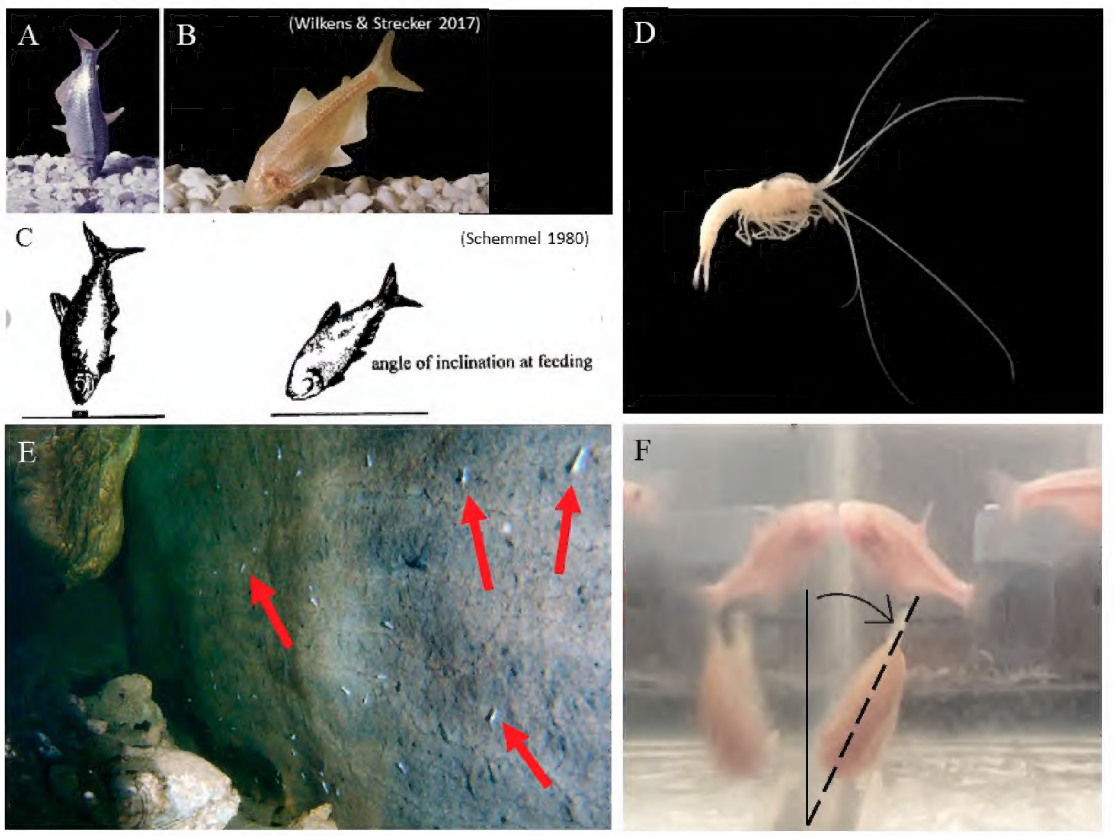


Figure 1. Feeding behavior on the floor and on the walls **A–C** *Astyanax* surface fish search for and pick up food lying on the ground at a high angle from the horizontal. Cavefish fed at lower angles (Modified from Wilkens and Strecker 2017 and Schemmel 1980) **D** in the field, Mysid shrimp are one of the sources of food for *Astyanax* **E** Mysid shrimp at Toro cave. Notice that mysid shrimp are mostly found crawling on the walls (four are highlighted by arrows) and seldom on the ground **F** *Astyanax* cavefish tilt their dorsoventral axis when cruising parallel to a glass wall in a tank they are acclimatized to live in.

by early investigators (Gertychowa 1970; Weissert and von Campenhausen 1981), and subsequently measured in numerous experiments (Teyke 1985, 1988, 1989; Abdel-Latif et al. 1990; Hassan 1992). Patton et al. (2010) then showed that wall-preference was unaffected by wall curvature regardless of being a straight, concave, or convex wall. Sharma et al. (2009) hypothesized that wall following has become more enhanced in blind morphs for exploratory purposes, in large part due to the enhanced, active-flow sensing abilities of the lateral line. In the videos used in Espinasa et al. (2021), it is notable that there is a preference for bottom of the pool or wall following in the native habitat by cavefish, although authors did not provide data as this was not the purpose of the paper.

The purpose of this study is to determine if cavefish and surface fish use a different posture when navigating by a wall. Feeding behavior and the way *Astyanax* cavefish navigates its surroundings in the absence of vision represent a captivating area of research that bridges the fields of ecology, biomechanics, and genetics.

Materials and methods

Field observations of sources of food

Most field studies conducted on *Astyanax* cavefish have been performed at sites accessible to bats and thus, bat guano has been reported as a main source of food (Espinasa

et al. 2017). However, many cavefish populations exist beyond sumps in underwater tunnels that are inaccessible to bats. We were interested in studying what are some of the potential food sources in these remote areas. For this, we performed an initial exploration in January 2020 at the deepest portion of Tinaja Cave in the Lake Room Siphon, and in February 2023 at Sabinos Cave in the section beyond Elliott's swim, which is connected to the main cave through a passage with just a few centimeters of air above the water. Both sections have less access to bats. Observations were done with snorkeling equipment and underwater lamps for scuba diving.

A third exploration took place in November 2023 to the Calera system, which has multiple sumps and underwater passages. In this case, remotely operated vehicles (ROV) were used to explore and capture videos. The underwater drone models used were the Fifish V6 and the Fifish V6s with a camera sensor of 1/2.3" SONY CMOS. Effective Pixels 12MP. ISO Range 100–6400 in Auto / Manual. Lens Field of View 166°. Aperture f/2.5. Min Focusing Distance 0.4 m. LED beams with a brightness of 4000 lumens. Two different underwater galleries beyond sumps were explored. One was 71 m long, and the other was 50 m. Attention was given to potential *Astyanax* food sources in these guano void regions of the cave. When found, it was recorded if they were preferentially localized on the floor or the walls. A description of the caves can be found in Elliott (2018) and Espinasa et al. (2020).

Dorsoventral axis angle

A 5-gallon fish tank was subdivided with a vertical glass. A Handycam DCR-SR42 Sony video camera was positioned perpendicular to the glass in such a way that fish swimming parallel to the glass wall would be swimming directly toward or away from the camera. In total, 16 Pachón cavefish (11 derived from the stock originally kept at Dr. Rohner's laboratory at the Stowers Institute and 5 from the stock originally kept at Dr. Borowsky's laboratory at NYU. Both stocks originated from different field collections), 17 Tinaja cavefish (Rohner's stock), 10 Choy River surface fish (Rohner's stock), and 4 eyeless surface fish (Rétaux's stock) were analyzed. Eyeless surface fish were obtained through lensectomy early in their development. Lens removal was conducted bilaterally in surface fish at 1 to 2 days post fertilization following the procedure outlined by Espinasa et al. (2023b). Eyeless fish were the same ones used in Espinasa et al. (2014).

Fish were left to acclimate for at least 30 minutes. Video recordings were made using the night vision function of the Handycam DCR-SR42 camera over a period of ten minutes, where for five minutes the fish were in the left compartment and five in the right compartment. Every time a fish swam parallel to the glass wall, a videoclip image would be extracted, pasted to PowerPoint, and the dorsoventral axis angle would be measured against the vertical angle. It was noted in each videoclip if the specimen was swimming with the right side or left side of its body towards the glass wall. A total of 170 video clips were analyzed for Pachón cavefish, 177 for Tinaja cavefish, 90 for surface fish, and 91 for eyeless surface fish.

A Mann-Whitney U test was used to establish if there was a difference in the average angle used by Pachón fish versus surface fish, Tinaja cavefish versus surface fish,

eyeless surface fish versus surface fish, and to establish if the angle used when specimens swam parallel to the wall with their left side, or the right side towards the wall was different for each of the three populations.

Results

Field observations of sources of food

With the use of an ROV, over 120 m of underwater passages were traversed at the Calera system. It was noticed that in galleries where there were no droppings from bats, one of the main potential sources of food was mysid shrimp, *Spelaeomysis quinterensis* (Fig. 1D). It was also noticed that mysid shrimp were predominately crawling on the walls and ceilings but infrequently on the floors (Fig. 1E). A similar pattern of mysid distribution was noticed when snorkeling at Tinaja and Sabinos (Kopp et al. 2018; Espinasa et al. 2020).

When foraging for bat guano, *Astyanax* can encounter this food by seeking on the surface, while droppings are still floating, or on the floor after the particles have sunk to the bottom. Our observations support that in underwater passages beyond the sumps, where bats can no longer reach, cavefish may have to navigate by the walls while seeking alternate sources of food in the way of aquatic crustaceans.

Dorsoventral axis angle

Surface fish and cavefish when navigating parallel to a wall use different dorsoventral axis body angles (Fig. 2A). Surface fish while in the dark swim parallel to the side of walls with a dorsoventral axis angle just slightly off from the vertical (average = 3.2° +/- 11.6° SD). On the contrary, cavefish incline the vertical axis of their body away from the wall (Figs 1F, 2C, D). Instead of their side being oriented parallel and towards the wall, their ventral underside is partially directed towards the wall and the dorsal back of their body is slightly away from the wall. Pachón cavefish incline their body 14.8° +/- 9.9° from the vertical and Tinaja cavefish 10.4° +/- 11.1°. Both Pachón and Tinaja cavefish swim with a significantly steeper angle than surface fish ($P < 0.00001$ for both).

Eyeless surface fish that were enucleated as embryos, and thus are accustomed to navigating without the use of vision throughout their lives, did not behave like cavefish ($P<0.00001$). They continued swimming with an angle similar to eyed surface fish in the dark (Fig. 2A). Their body axis angle (3.1° +/- 6.5°) was almost vertical and not significantly different from the eyed surface in the dark ($P = 0.560$).

In both Pachón and Tinaja cavefish, when their right side of the body is toward a wall, the angle of inclination is significantly higher than when their left side is towards a wall (Fig. 3). Pachón right = 16.6° +/- 10.2° versus Pachón left = 12.9° +/- 9.3° ($P = 0.012$). Tinaja right = 12.6° +/- 9.6° versus Tinaja left = 7.8° +/- 12.2° ($P = 0.012$). Surface fish did not have a significantly different angle of inclination between sides. Surface right = 6.1° +/- 9.7° versus Surface left = 1.0° +/- 12.5° ($P = 0.214$).

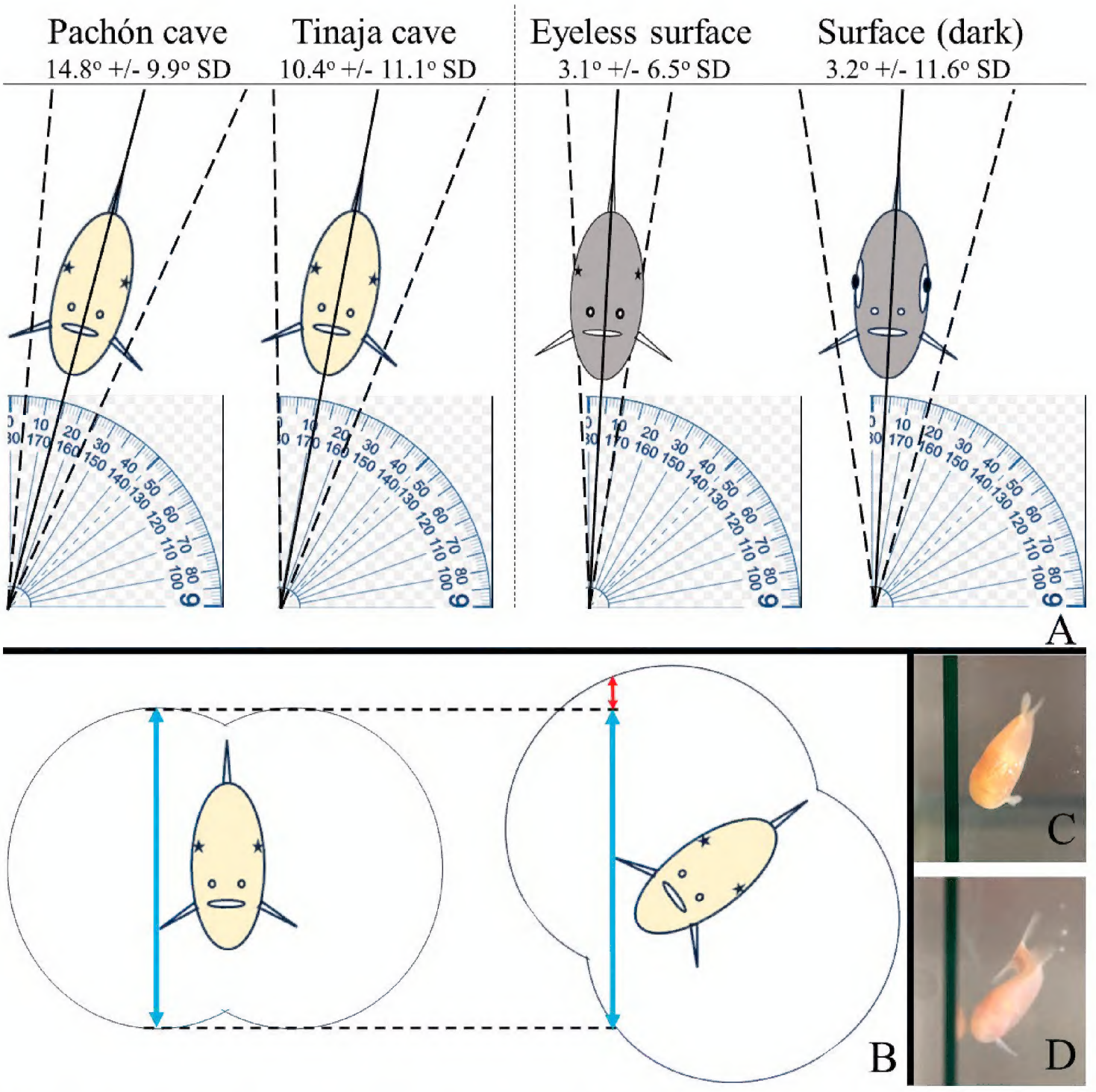
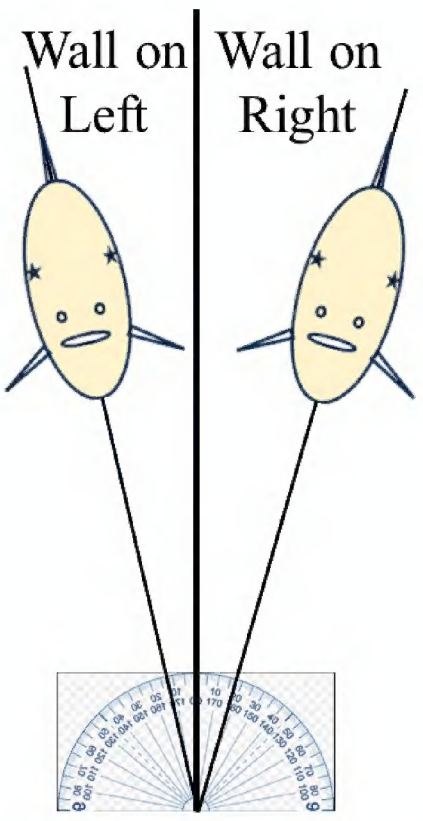


Figure 2. Dorsoventral axis when swimming by a wall **A** when swimming by a wall, cavefish from both Pachón and Tinaja caves incline the vertical axis of their body away from the wall. Eyeless surface fish enucleated as embryos, and surface fish in the dark do not incline as much their vertical axis and swim with a mostly vertical dorsoventral axis. Dotted line = standard deviation from average. Black star = eyeless. **B** When swimming vertically by the side of a wall, the detection field indicated by the semi-sphere on one side of the body can scan an area of the wall (Left; blue arrow). When tilted, a portion of the other side of the body's receptive field or sensory space enlarges the total area of the wall that can be scanned (Blue + red arrow) **C, D** two Pachón cavefish swimming by a glass wall, with the distinct tilt of their dorsoventral axis.

Discussion

Previous studies have shown that bat guano constitutes one of the main sources of nourishment for adult cavefish in passages inhabited by bats (Espinasa et al. 2017). Given that a large portion of the cavefish habitat is in underwater passages beyond sumps, which bats cannot have access to, we used an underwater drone to explore these passages inaccessible to humans without the use of scuba equipment. Our field observations have



	Right	Left	P value
Pachón	16.6° +/- 10.2° N=88	12.9° +/- 9.3° N=82	P=0.012
Tinaja	12.6° +/- 9.6° N=95	7.8° +/- 12.2° N=82	P=0.002
Surface	6.1° +/- 9.7° N=39	1.0° +/- 12.5° N=51	P=.214

Figure 3. When cavefish swim with their right side of the body toward a wall, the angle of inclination is significantly higher than when their left side is towards a wall. Average angles used by Pachón fish are portrayed in the drawing.

shown that in these areas, *Spelaeomysis quinterensis* is very abundant. In the laboratory, *Astyanax* are avid eaters of commercial mysid shrimps and in the field, when a mysid shrimp was deposited in a tank with a cavefish (Espinasa et al. 2020), it was eventually eaten, thus supporting that fish consume mysid shrimp in the field. Of note, it was observed that these mysid shrimps were predominately crawling on the walls and ceilings, but seldom crawling on the floor. As part of their adaptation to the darkness of the underground, cavefish must have evolved a more efficient way to navigate by the walls, and a more efficient foraging behavior when seeking such prey that is not on the floor.

Cavefish can build hydrodynamic images of their surroundings (Windsor et al. 2010). They swim near the walls gliding alongside them, sensing detailed information about objects by the changes in the flow field around their body using their lateral line sensory system (Windsor et al. 2010). Cavefish and surface fish use different angles with respect to the horizontal when searching for food on the ground (Schemmel 1980). Hence, in our study, the angle of the body axis with respect to a vertical wall was measured while fish swam in a tank. Results show that when swimming by a wall, cavefish tilt the vertical axis of their body away from the wall (Fig. 1F). This inclination of the angle of the body axes was significantly higher than surface fish (Fig. 2A).

Why would they incline their body? Espinasa et al. (2023a) described the position and distance from prey when performing a strike during Larval Prey Capture (LPC) behavior. They provided a mathematical model that included a receptive field or sensory detection range as two semi-circles or spheres on each side of the body. At this point, we hypothesize that when swimming vertically by the side of a wall, only the receptive field of one side of the body can scan an area of the wall (Fig. 2B). But when the body is

inclined, a portion of the other side of the body's receptive field enlarges the total area of the wall that can be scanned (Fig. 2B). Future studies may confirm this hypothesis.

Results also showed that there was a laterality in the way that cavefish inclined the body axis when swimming by a wall. Both Pachón and Tinaja cavefish used a significantly higher angle when their right side of the body is toward a wall than when their left side is towards a wall (Fig. 3). Previous studies have shown that cavefish have a laterality of "handedness" during foraging behavior. In the field, cave populations preferentially circle to the right side or the left side around a source of vibrations (Espinasa et al. 2022). Likewise, in LPC behavior, cavefish larvae from different populations strike at prey that is preferentially on their right side or their left side (Espinasa et al. 2023a). In the laboratory, individuals from Tinaja Cave showed a moderately consistent preference in VAB for left- or right-side approaches (Fernandes et al. 2022). There may be physiologic or morphologic reasons for this behavioral laterality. For example, there is a positive correlation between the VAB level and the number of left- but not right-side superficial neuromasts in Pachón cavefish (Fernandes et al. 2018). Also, cavefish exhibit directional "bends" in skull shape (Fig. 4A), almost always biased to the left (Powers et al. 2017).

Why would cavefish show a laterality in the way they tilt the body axis when one side of the body or the other is towards a wall? When Espinasa et al. (2023a) described the position and distance from prey when performing a strike during LPC behavior, they proposed in their mathematical model that the receptive field on each side of the body had different radii. The number of strikes shows an enhanced performance for one side, suggesting that each of the receptive field semi-spheres on each side of the body has different volumes (Fig. 4B). As before, we suggest here a hypothesis that will require confirmation in future research. We assume that when cavefish swim with their right side towards a wall, which presumably has a smaller receptive field, if the fish tilts its body to make use of the other side of the body's receptive field, it would enhance its performance (Figs 2B, 4B). But if their left side of the body is towards the wall, which presumably has a larger receptive field, the fish would gain comparatively less enhanced performance by tilting their body axes (Fig. 4C). Future studies may again confirm this hypothesis.

Conclusion

When swimming by a wall, surface fish in the dark and eyeless surface fish swim with a dorsoventral axis angle mostly vertical. On the contrary, cavefish tilt the vertical axis of their body away from the wall. It is hypothesized that when cavefish tilt their body angle, a portion of the other side of the body's receptive field or sensory detection range enlarges the total area of the wall that can be scanned (Fig. 2B). It is also hypothesized that asymmetries in the function of the superficial neuromasts, the bent shape of the cavefish skull, and/or other morphologic of physiologic asymmetries contribute to creating differently sized reception fields on either side of the body. This could explain the different tilt in angle when swimming with their left side or right side of the body towards the wall.

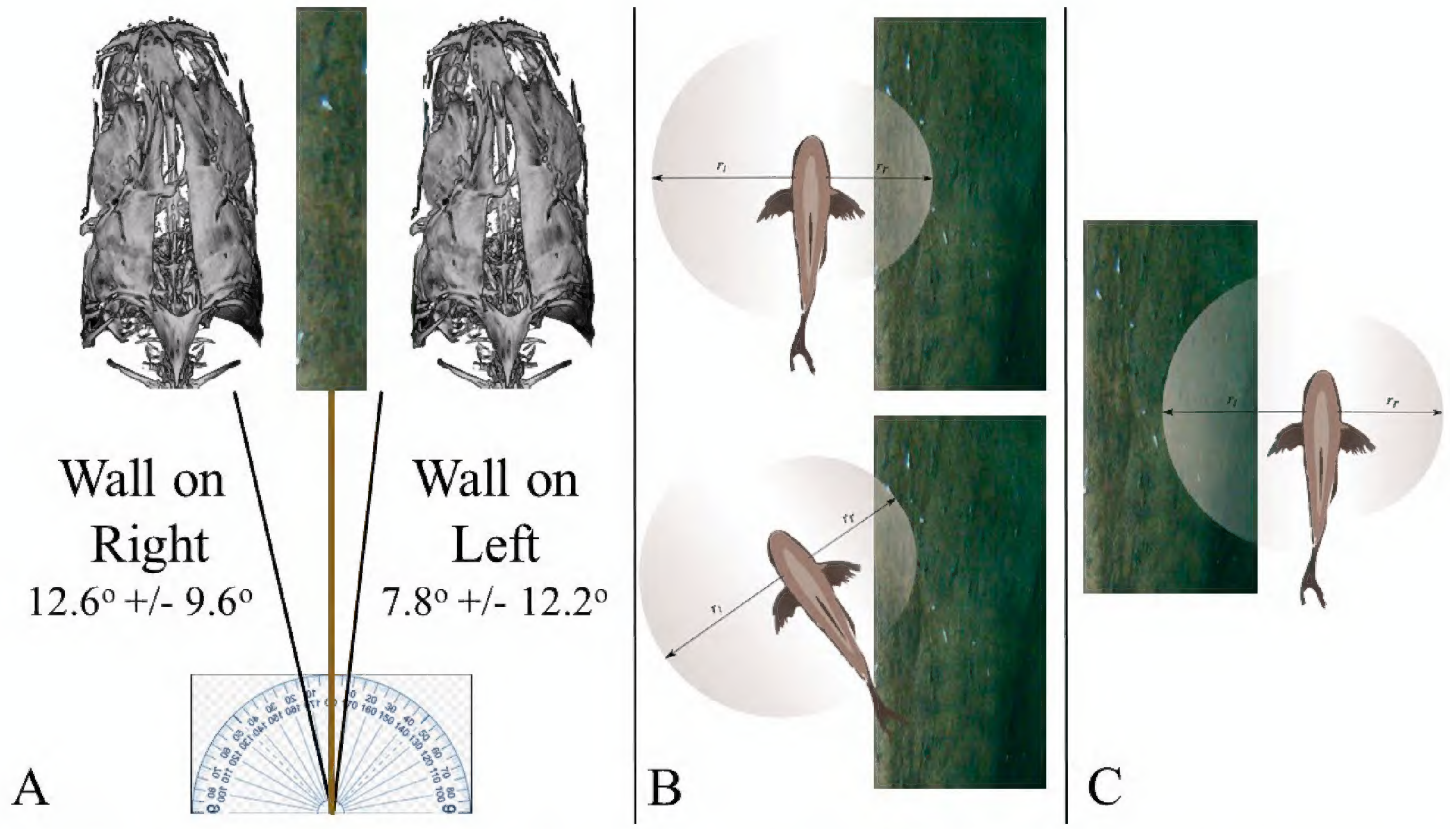


Figure 4. Hypothesis for asymmetrical dorsoventral axis swimming by a wall **A** cavefish have a leftward-biased dorso-cranial bend, where the concave side of the head is towards their left side (Powers et al. 2017). Likewise, Pachón cavefish show a positive correlation of VAB with the number of neuromasts on their left side but not on their right (Fernandes et al. 2018). Results from this study show that when cavefish swim with their left side of the body toward a wall (grey rectangle with white mysid shrimps), the angle of inclination is significantly less than when their right side is towards a wall. Average angles used by Tinaja fish and Tinaja skulls are portrayed in the drawing. By leaning their underside towards the wall (**B**) cavefish receptive fields (grey semicircles with different radii: *Rr=right* and R_l*=left*) from both sides of the body may be combined to increase surface area scanned. Espinasa et al. (2023a) showed that receptive fields on either side of the body in cavefish are asymmetric. It is hypothesized that when cavefish swim with their smaller receptive field (**B**) towards a wall, increasing the dorsoventral axis angle provides a proportionally higher scanned surface area than when cavefish swim with their larger receptive field (**C**) towards the wall. In this case, it is expected that a larger angle will be used when swimming with their right side of the body towards the wall than when their left side is towards the wall.

Conflict of interest

The authors have declared that no competing interests exist.

Acknowledgments

Michael Sandone and Michael Girard are the technical specialists and drivers of the remotely operated vehicle (ROV). Without their participation, underwater passages could not have been explored. Thanks to all group members who participated in the January 2020 and February 2023 field trips. In particular Patricia Ornelas and Sylvie Rétaux. This study was supported by the School of Sciences of Marist College.

References

Abdel-Latif H, Hassan ES, Campenhausen C (1990) Sensory performance of blind Mexican cave fish after destruction of the canal neuromasts. Naturwissenschaften 77: 237–239. https://doi.org/10.1007/BF01138492

Elipot Y, Hinaux H, Callebert J, Launay JM, Blin M, Rétaux S, Yann Y (2014) A mutation in the enzyme monoamine oxidase explains part of the *Astyanax* cavefish behavioural syndrome. Nature Communications 5: 3647. https://doi.org/10.1038/ncomms4647

Elliott WR (2018) The *Astyanax* caves of Mexico: Cavefishes of Tamaulipas, San Luis Potosi, and Guerrero. AMCS Bulletin 26: 1–325.

Espinasa L, Bibliowicz J, Jeffery WR, Rétaux S (2014) Enhanced prey capture skills in *Astyanax* cavefish larvae are independent from eye loss. EvoDevo 5(1): 1–7. https://doi.org/10.1186/2041-9139-5-35

Espinasa L, Bonaroti N, Wong J, Pottin K, Queinnec E, Rétaux S (2017) Contrasting feeding habits of post-larval and adult *Astyanax* cavefish. Subterranean Biology 21: 1–17. https://doi.org/10.3897/subtbiol.21.11046

Espinasa L, Ornelas-García CP, Legendre L, Rétaux S, Best A, Gamboa-Miranda R, Espinosa-Pérez H, Sprouse P (2020) Discovery of two new *Astyanax* cavefish localities leads to further understanding of the species biogeography. Diversity 12(10): 368–389. https://doi.org/10.3390/d12100368

Espinasa L, Heintz C, Rétaux S, Yoshisawa M, Agnès F, Ornelas-Garcia P, Balogh-Robinson R (2021) Vibration attraction response is a plastic trait in blind Mexican tetra (*Astyanax mexicanus*), variable within subpopulations inhabiting the same cave. Journal of Fish Biology 98(1): 304–316. https://doi.org/10.1111/jfb.14586

Espinasa L, Diamant R, Mesquita M, Lindquist JM, Powers AM, Helmreich J (2022) Laterality in cavefish: Left or right foraging behavior in *Astyanax mexicanus*. Subterranean Biology 44: 123–138. https://doi.org/10.3897/subtbiol.44.86565

Espinasa L, Diamant R, Vinepinsky E, Espinasa M (2023a) Evolutionary modifications of *Astyanax* larval prey capture (LPC) in a dark environment. Zoological Research 44(4): 750. https://doi.org/10.24272/j.issn.2095-8137.2022.466

Espinasa L, Pavie M, Rétaux S (2023b) Protocol for lens removal in embryonic fish and its application on the developmental effects of eye regression. Subterranean Biology 45: 39–52. https://doi.org/10.3897/subtbiol.45.96963

Fernandes VFL, Macaspac C, Lu L, Yoshizawa M (2018) Evolution of the developmental plasticity and a coupling between left mechanosensory neuromasts and an adaptive foraging behavior. Developmental Biology 441(2): 262–271. https://doi.org/10.1016/j.ydbio.2018.05.012

Fernandes VFL, Glaser Y, Iwashita M, Yoshizawa M (2022) Evolution of left–right asymmetry in the sensory system and foraging behavior during adaptation to food-sparse cave environments. BMC biology 20(1): 295. https://doi.org/10.1186/s12915-022-01501-1

Gertychowa R (1970) Studies on the ethology and space orientation of the blind cave fish *Anoptichthys jordani* Hubbs et Innes 1936 (Characidae). Folia Biologica 18: 9–69.

Hassan ES (1992) Mathematical description of the stimuli to the lateral line system of fish derived from a three-dimensional flow field analysis. II. The case of gliding alongside

or above a plane surface. Biological Cybernetics 66: 453–461. https://doi.org/10.1007/BF00197726

Kopp J, Avasthi S, Espinasa L (2018) Phylogeographical convergence between *Astyanax* cavefish and mysid shrimps in the Sierra de El Abra, Mexico. Subterranean Biology 26: 75–84. https://doi.org/10.3897/subtbiol.26.27097

Kowalko JE, Rohner N, Linden TA, Rompani SB, Warren W, Borowsky R, Tabin CJ, Jeffery WR, Yoshizawa M (2013) Convergence in feeding posture occurs through different genetic loci in independently evolved cave populations of *Astyanax mexicanus*. Proceedings of the National Academy of Sciences 110(42): 16933–16938. https://doi.org/10.1073/pnas.1317192110

Patton P, Windsor S, Coombs S (2010) Active wall following by Mexican blind cavefish (*Astyanax mexicanus*). Journal of Comparative Physiology A 196: 853–867. https://doi.org/10.1007/s00359-010-0567-8

Powers AK, Davis EM, Kaplan SA, Gross JB (2017) Cranial asymmetry arises later in the life history of the blind Mexican cavefish, *Astyanax mexicanus*. PLoS One 12(5): p.e0177419. https://doi.org/10.1371/journal.pone.0177419

Schemmel C (1980) Studies on the genetics of feeding behaviour in the cave fish *Astyanax mexicanus* f. *Anoptichthys*: an example of apparent monofactorial inheritance by polygenes. Zeitschrift für Tierpsychologie 53(1): 9–22. https://doi.org/10.1111/j.1439-0310.1980.tb00730.x

Sharma S, Coombs S, Patton P, Burt de Perera T (2009) The function of wall-following behaviors in the Mexican blind cavefish and a sighted relative, the Mexican tetra (*Astyanax*). Journal of Comparative Physiology A 195: 225–240. https://doi.org/10.1007/s00359-008-0400-9

Teyke T (1985) Collision with and avoidance of obstacles by blind cave fish *Anoptichthys jordani* (Characidae). Journal of Comparative Physiology A 157: 837–843. https://doi.org/10.1007/BF01350081

Teyke T (1988) Flow field, swimming velocity and boundary layer: parameters which affect the stimulus for the lateral line organ in blind fish. Journal of Comparative Physiology A 163: 53–61. https://doi.org/10.1007/BF00611996

Teyke T (1989) Learning and remembering the environment in the blind cave fish *Anoptichthys jordani*. Journal of Comparative Physiology A 164: 655–662. https://doi.org/10.1007/BF00614508

Weissert R, von Campenhausen C (1981) Discrimination between stationary objects by the blind cave fish *Anoptichthys jordani*. Journal of Comparative Physiology A 143: 375–381. https://doi.org/10.1007/BF00611176

Windsor SP, Norris SE, Cameron SM, Mallinson GD, Montgomery JC (2010) The flow fields involved in hydrodynamic imaging by blind Mexican cave fish (*Astyanax fasciatus*). Part II: gliding parallel to a wall. Journal of Experimental Biology 213(22): 3832–3842. https://doi.org/10.1242/jeb.040790

Yoshizawa M, Gorički Š, Soares D, Jeffery WR (2010) Evolution of a behavioral shift mediated by superficial neuromasts helps cavefish find food in darkness. Current Biology 20(18): 1631–1636. https://doi.org/10.1016/j.cub.2010.07.017